AVIAN BIOGEOGRAPHY OF THE GREAT BASIN AND INTERMOUNTAIN REGION

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ABSTRACT.—There are no endemic species of birds in the Great Basin. Nevertheless, a distinctive Great Basin avifauna exists which contains components of the Mojave Desert, Rocky Mountain, and Great Plains avifaunas as well as species obligate to sagebrush and the pinyon-juniper forest. Seemingly there has been little spread of California and Sierra Nevada species eastward, but a westward extension from the Rocky Mountains of several species is indicated. While several Rocky Mountain species reach their western limits on the eastern edge of the Great Basin, others have extended into the eastern portion. Two Great Plains representatives are late arrivals, namely the Baltimore Oriole and Indigo Bunting, with evidence of introgression now occurring with related western species. A similar but longstanding situation exists for the flickers. A zone of hybridization occurs in northern Utah between two species of junco. A rather abrupt junction zone between the Great Basin and Mojave Desert avifaunas exists in southern Nevada and extreme southwestern Utah. Several species representing the Mojave Desert avifauna have extended their ranges in recent years into southern Utah. Geographically variable birds show diverse patterns of distribution along with much clinal variation and intergradation. A center of differentiation for four species occurs in western Utah in the eastern portion of the Great Basin while two more occur in the western portion of the basin. The Wasatch Front is a dividing area between western and eastern races in several species. Extreme southwestern Utah constitutes a transition area where several species are represented by different races or intergradational populations. A study of the avifaunas of 14 boreal "islands" in isolated mountain ranges in western and southeastern Utah in comparison with the Rocky Mountain "continent" in central and northern Utah shows a close correlation between number of species present and habitat diversity. In addition, a low correlation exists between the number of species that are permanent residents on isolated mountains and the distance of those mountains from the "continent."

Biogeography is concerned with the distribution of organisms in time and space. Applying this to birds and the Great Basin region, it is the consensus among students of avian paleontology that most species of modern birds arose during the Pleistocene (Selander 1965), but there is virtually no fossil record of birds for the Great Basin during that interval of time. Trimble and Carr (1961) mention that bones of birds as well as of several kinds of mammals and molluscs have been found in gravel overlying the Raft Formation of American Falls Lake bed in southern Idaho which represent the late Quaternary, but no identities of the birds are given. A number of bird bones associated with prehistoric human habitations in caves in the Great Basin have been found, two of the best-known sites being Danger Cave near Wendover (Jennings 1957) and Hogup Cave near the northwestern corner of Great Salt Lake (Aikens 1970), but all the bird bones and feathers represent living species. Hall (1940) describes an ancient nesting site of White Pelicans at Rattlesnake Hill on the northeastern edge of the town of Fallon, Nevada, containing bones of White Pelicans, Double-crested Cormorants, and a Canada Goose. The bones were situated beneath a water-formed calcareous layer, which indicated that the bones had been under water at least once; but whether this was before, at, or after the time when Lake Lahonton attained its maximum level was not ascertained. The implication from the find is that the avian associates in this prehistoric time were about the same as one finds today at the colony on Anaho Island in nearby Pyramid Lake. Despite the virtual absence of a

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fossil record, it is probably safe to assume that the species of birds present in the Great Basin in the Quaternary were essentially the same as those present in the region today. With different climatic conditions, however, from time to time there have doubtless been different assemblages of birds and different distributional patterns than are seen at present. Thus, in the absence of a fossil record for the region under consideration, reliance must be placed on an analysis of the distribution of today's species in the search for clues to dispersal routes and subspecific differentiation.

Before considering the spatial dimension of the biogeography of birds of the region under consideration, it may be well to note two special items in connection with birds. One is that some birds are migratory. Thus a distinction must be made between summer residents and permanent residents. The migratory summer residents are able to easily traverse distances between mountain ranges and so are less subject to the effects of isolation than are the sedentary permanent residents. The second point is that there is a wealth of data pertaining to the distribution of birds in the collections of many museums, with much of the data readily available in published reports. For the region under consideration the following constitute the principal sources of information on the distribution of birds: for California, Grinnell and Miller (1944); for Nevada, Linsdale (1936 and 1951) and Johnson (1965, 1973, 1974); for Idaho, Burleigh (1972); for Utah, Behle (1943, 1955, 1958, 1960), Behle, Bushman and Greenhalgh (1958), Behle and Ghiselin (1958), Behle and Perry (1975), and Hayward, Cottam, Woodbury, and Frost (1976); for Colorado, Bailey and Niedrach (1965). Phillips (1958) has discussed many special problems having to do with the collecting of birds and the shortcomings of museum collections. Even though the material available falls short of the need, birds are still one of the best known groups of animals in terms of biogeography.

Great Basin Avifauna

Turning now to the spatial dimension, an important initial consideration is whether there is a distinctive avifauna in the Great Basin. Are the kinds of birds that occur in western Utah and Nevada different en masse from those found in the California-Sierra Nevada region on the west or the Colorado-Rocky Mountain region to the east? This query pertains only to land birds, since water birds are widespread in their occurrence throughout North America and generally show few regional distinctions except for relative abundance of particular species. An analysis of the distribution of the land birds indicates that the great majority that occur in the Great Basin range widely throughout western North America. There are about 154 kinds of resident birds in this wide-ranging category. Any distinctions, then, pertain to a relatively few kinds, but mostly it is a matter of a different combination of species in the Great Basin as compared with the assemblages in neighboring regions. Udvardy (1963: 1157) includes a Great Basin avifauna in his treatment of the bird faunas of North America, stating that the species fall geographically and ecologically into two groups, namely (1) the sagebrush-arid woodland faunal group and (2) the northwestern arid woodland faunal group. Miller (1951) in his analysis of the distribution of the birds of California includes a Great Basin avifauna as one of four faunal groups represented in the state, one that is intrusive into northeastern California east of the Sierran crest. He states that the Great Basin avifauna consists of two categories: (1) species of interior continental derivation that occur south of or below the boreal areas, and (2) geographic races that have differentiated in the Great Basin at austral levels. He designates 35 kinds as belonging to the Great Basin avifauna. Johnson (1975) followed Miller in his treatment of a Great Basin avifauna.

Probably the most distinctive feature about the Great Basin avifauna is the presence of certain birds that are associated with two plant formations that occur widely throughout the region, namely big sage (*Artemisia tridentata*) and the pinyon-juniper woodland. Birds that occur almost exclusively in stands of sagebrush are the Sage Grouse, Sage Thrasher, and Sage Sparrow. Birds that occur chiefly, if not exclusively, in the pygmy woodland, which itself has much sage interspersed with the junipers and pinyon pines, are the Cassin's Kingbird, Gray Flycatcher, Scrub Jay, Pinyon Jay, Plain Titmouse, Bush-tit, Blue-Gray Gnatcatcher, Cedar Waxwing, Gray Vireo, Black-throated Gray Warbler, and Brewer's Sparrow. However, the pygmy woodland occurs throughout the Southwest so these associated species of birds occur in areas beyond the Great Basin. To properly characterize the Great Basin avifauna, comparisons with surrounding regions are necessary.

There are about 30 kinds of distinctive birds that occur in the California-Pacific Coast-Sierra Nevada region that are not known to occur in either the Great Basin or the Rocky Mountains. Many are endemic to the West Coast area and constitute the most conspicuous elements of the California avifauna. Some of these, such as the Mountain Quail and White-headed Woodpecker, occur in the Sierra Nevada on the western rim of the Great Basin, but I find little evidence of these distinctive California forms spilling over eastward into the mountain ranges in the Great Basin. Several northern birds reach the southern limits of their ranges, at least in part in the Great Basin. These are the Marsh Hawk, Roughed Grouse, Sharp-tailed Grouse, Sage Grouse, Lewis Woodpecker, Tree Swallow, Swainson's Thrush, Water Pipit, American Redstart, and Fox Sparrow. Many southern birds reach their northern limits, in at least part of their range, in the Great Basin. These are the Whip-poor-will, Black Phoebe, Gray Flycatcher, Plain Titmouse, Bewick's Wren, Bendire's Thrasher, Blue-gray Gnatcatcher, Gray Vireo, Virginia's Warbler, Black-throated Gray Warbler, Painted Redstart, Scott's Oriole, Lesser Goldfinch, Black-throated Sparrow, Gray-headed Junco, and Black-chinned Sparrow. There are about 25 kinds representing the Mojave Desert avifauna that occur in southeastern Nevada and southwestern Utah but which do not penetrate any farther north into the Great Basin except on an accidental basis. These are discussed in the following section of this paper.

Nineteen kinds of birds occur in Colorado that do not occur as breeders in either the Great Basin or California areas. Mostly these are species of the Great Plains avifauna that reach the western limits of their ranges along the east base of the Rocky Mountains. One species is endemic to the mountains of Colorado, namely the Gray-crowned Rosy Finch. There are several species that occur as breeders in both the Rocky Mountains and the Great Basin which do not occur in the California-Sierra Nevada area. Thus they reach their western limits within the Great Basin. These are the Northern Three-toed Woodpecker, Catbird, Brown Thrasher, Veery, Water Pipit, Black Rosy Finch and Indigo Bunting. None of these are common in the Great Basin and at least two, the Brown Thrasher and Indigo Bunting, appear to be late arrivals in the region west of the Rocky Mountains. Three species are found at the eastern edge of the Great Basin in Utah but are not known to occur in the basin per se. These are the Purple Martin, Gray Jay, and Pine Grosbeak. Several kinds are essentially restricted in Utah in their breeding range to the Colorado River drainage system, but occasionally individuals occur in the Great Basin as accidentals. These are the Gambel Quail, Costa Hummingbird, Roadrunner, Bendire's Thrasher, and Blue Grosbeak. Finally, I know of no species of bird that is endemic to the Great Basin.

From all this we can conclude that there is a distinctive Great Basin avifauna but it is one that is not characterized by endemic species. Rather it is recognizable on the basis of a different assemblage of birds, many of which are intrusive from surrounding regions. There is more evidence of a western spread of eastern species into the Great Basin than there is of an eastward spread from the Sierra Nevada-California area. Because of the lack of endemics, the Great Basin avifauna is not as distinctive as surrounding avifaunas, but it is more sharply confined, being delimited on the west by the Cascade-Sierra cordillera and on the east by such outlying ranges of the Rockies as the Wasatch Mountains of northern Utah and the high plateaus of central Utah. On the south the Great Basin avifauna meets the Mojave Desert avifauna in a rather distinct and narrow junction zone. There is no comparable junction zone or mountain barrier at the northern limits of the Great Basin. Here the Great Basin species gradually merge with those of either the western woodland edge or those of the open Palouse country east of the Cascades.

Relations of Mojave Desert and Great Basin Avifaunas in Southwestern Utah and Southeastern Nevada

The northern limits of the Mojave Desert Biome in Nevada have been mapped by Gullion et al. (1959: 279). Areas included are Meadow Valley Wash, Muddy River, and Pahranagat Valley. In southwestern Utah, the warm southern desert occurs along the floor of the Virgin River Valley to the mouth of Zion Canyon near Springdale (including Coal Pits Wash) as well as along the lower stretches of tributary streams such as La Verkin, Ash, and Santa Clara creeks and Beaver Dam Wash on the west side of the Beaver Dam Mountains. In Arizona it occurs along the Virgin River Valley. There are 28 kinds of summer resident birds in this region that are representatives of the Mojave Desert avifauna. Fifteen of these are known to occur in Utah only in this area. The other 13 occur there regularly but a few extralimital records exist elsewhere in the state. The Mojave Desert avian indicators are the Black Hawk, Gambel's Quail, White-winged Dove, Ground Dove, Inca Dove, Roadrunner, Lesser Nighthawk, Costa's Hummingbird, Rivoli's Hummingbird, Ladderbacked Woodpecker, Wied's Crested Flycatcher, Black Phoebe, Vermilion Flycatcher, Verdin, Cactus Wren, Le Conte's Thrasher, Crissal Thrasher, Black-tailed Gnatcatcher, Phainopepla, Bell's Vireo, Lucy's Warbler, Painted Redstart, Hooded Oriole, Scott's Oriole, Summer Tanager, Blue Grosbeak, Abert's Towhee, and Rufous-crowned Sparrow. Several of these species seem to have extended their ranges into southwestern Utah in recent years, namely, the Black Hawk, White-winged Dove, Inca Dove, Rivoli's Hummingbird, Wied's Crested Flycatcher, Black-tailed Gnatcatcher, Summer Tanager, and possibly the Rufous-crowned Sparrow, although the latter may represent an overlooked species associated with a relict grassland habitat. A summary of records and details of distribution for this complement of birds has recently been presented by Behle (1976b) for the three-state region. Immediately to the north of this Mojave Desert or Lower Sonoran area and at higher elevations in the region in the pinyon-juniper belt, birds are found that represent the Great Basin avifauna.

There are some aspects of subspecies distribution and intergradation in extreme southwestern Utah that are significant in terms of southern derivations of the population. These are discussed elsewhere in this paper. The hybridization that produces intergradation in these several species, as well as increased variability in the populations, suggests the presence of a suture zone, using the terminology of Remington (1968). He defined a suture zone as "a band, whether narrow or broad, of geographic overlap between major biotic assemblages, including some pairs of species or semispecies which hybridize in the zone." As Uzzell and Ashmole (1970) further note, suture zones stand to biotas as zones of secondary intergradation stand to pairs of populations. Unless one prefers to regard the Gilded Flicker as a separate species from the Red-shafted Flicker, to my knowledge no hybridization occurs in extreme southwestern Utah at the species level. Rather, the crossing is between representatives of different subspecies producing intermediate and highly variable populations where, in addition to the intergrades, typical representatives of the two parental stocks occur. In the region to the north of the Virgin River Valley, some cases are known where introgression has taken place. These are discussed in another section of this paper.

Boreal Islands and Effects of Isolation

One of the most significant aspects of zoogeography in the Great Basin and Intermountain Region pertains to the discontinuous occurrence of boreal species on the many isolated mountaintops of the region. The distribution of birds on 31 such islands has been discussed by Johnson (1975) in a study patterned after similar studies by Brown (1971) on mammals of the Great Basin ranges and Vuilleumier (1970) on birds in the páramo islands in the northern Andes. Although Johnson had data available from several of my reports for certain islands in western Utah which constituted the eastern fringe of his study area, additional data for Utah have been mobilized for this paper to extend Johnson's study. Although I have followed his procedures, our data are not precisely comparable because of regional differences in the avifauna, my elimination of water birds from the boreal category, and the circumstance that I have followed Brown's approach of considering as boreal species those that occur above 7500 feet elevation rather than attempting to determine the lower edge of the forest woodland. The 80 species that I have designated as boreal are listed in the Appendix along with an indication of their presence or absence on the 14 boreal islands studied in western and southeastern Utah. The basic data for the several islands are presented in Table 1. These data were first subjected to a normality check which showed that they fit a normal distribution in an untransformed condition. The data were then analyzed by means of a partial correlation analysis which showed that three variables, namely elevation of highest peak, total area, and habitat diversity score (HDS) were highly correlated. Then a stepwise multiple regression study showed that HDS had the highest correlation with the total number of bird species occurring. The R-value (correlation coefficient) was .86, which was significant at the .001 level. Because of the intercorrelation among the three independent variables, the multiple regression analysis was run first with HDS included in the equation while excluding elevation and total area. Then it was run excluding HDS but including elevation and area. Finally calculations were made including all three variables. As is indicated by the data summarized in Table 3 and the adjusted R^2 values, the effect of multicolinearity is present when all three variables are included in the equation. Although not as strong, these results follow those of Johnson closely. Because of the multicolinearity when all three independent variables were included in the equation, the R^2 value given in Figure 2 (which is .75) is the value derived from the equation excluding elevation and total area. The results shown in Figure 2 are similar to those of Johnson (1975: 553).

Although there is a high correlation between the number of kinds of birds occurring and general habitat diversity as represented by the habitat diversity scores, there is the complication that the HDS involves many environmental variables. In attempting to identify particular aspects of the habitat community structure that control the kinds and number of species present, Johnson (1975: 555) analyzed the species composition of the boreal birds and their ecologic rolls in the community. He divided them into two groups: "Restricted," which occurred in 5 or fewer of his 31 sample areas,

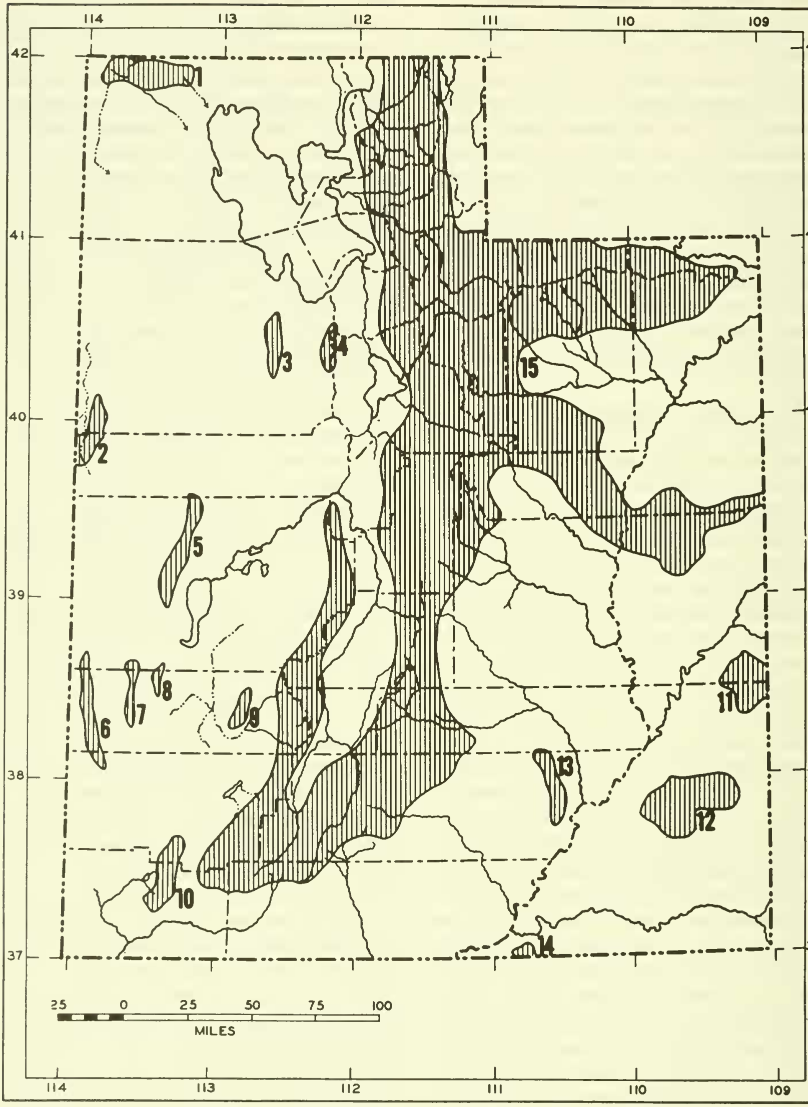

Fig. 1. Map of Utah showing locations of Boreal Islands and Rocky Mountain Continent area above 7500 feet elevation. 1. Raft River Mts., 2. Deep Creek Mts., 3. Stansbury Mts., 4. Oquirrh Mts., 5. House Range, 6. Needle Range, 7. Wah Wah Mts., 8. Frisco Mts., 9. Mineral Mts., 10. Pine Valley Mts.,11. La Sal Mts., 12. Abajo Mts.—Elk Ridge, 13. Henry Mts., 14. Navajo Mtn., 15. Wasatch-Uinta-Tushar-High Plateau Continent.

and "Standard," which occurred in 28 or more. Birds in the "Standard" category are presumed to have generalized boreal requirements in contrast to specialized requirements for the "Restricted" group. Johnson noted Willson's (1974) work that deals with aspects of habitat structure in relation to species and numbers of birds. A more recent paper along similar lines is Flack's (1976) study of bird populations in the aspen forests in western North America. The approach of Willson and Flack focuses attention on the significance of particular environmental variables presently covered by Johnson's habitat diversity score.

The next highest correlation shown by my data is with width of barrier, but this is significant only in connection with the category of permanent residents (R = .43). In other words, for the summer residents there is no correlation between number of kinds occurring on an island and distance from the nearest island or continent, while for the permanent residents the number of kinds decreases with remoteness from the continental area. The distance correlation is minor, however, compared with that for habitat diversity. Again my results are essentially the same as those of Johnson (1975). He expressed the opinion that the distance factor in the case of birds operates through impoverishment of habitat rather than through ease of access.

A low correlation shows up for my data between number of species and total area of the island (see Table 2). This is contrary to the results of both Brown and Johnson as well as the postulate of MacArthur and Wilson (1963, 1967) that area and environmental diversity are closely related and that total area serves as a good general predictor of habitat variety. The lack of correlation between number of species and size of area for the islands that I studied was probably influenced by the disparate results for the two smallest islands, namely the Frisco Mountains with a size of 11 square miles and only 19 kinds of birds as compared to Navajo Mountain with 13 square miles and 49 kinds of birds. I gave a habitat diversity score of 3 to the Frisco Mountain area and a 5 to Navajo Mountain. The Frisco range is very dry and has a sparse coniferous forest. Navajo Mountain is also lacking in surface accumulation of water, yet supports much more forest covering. Environmental

TABLE 1. Data for Boreal Islands and the Rocky Mountain Mainland in Utah.*

Area No.	Mountain Range	N_1	N_2	N_3	AR	WB	DM	EHP	LHP	HDS
1	Raft River Mts.	61	22	39	64	48	79	9892	41.92	10
2	Deep Creek Mts.	52	20	32	223	9	104	12101	39.83	11
3	Stansbury Mts.	44	18	26	54	16	39	11031	40.27	8
4	Oquirrh Mts.	50	20	30	82	16	19	10676	40.22	9
5	House Range	25	9	16	25	35	63	9725	39.09	4
6	Needle Range	29	10	19	92	11	65	9783	38.16	4
7	Wah Wah Mts.	42	15	27	54	11	53	9065	38.33	6
8	Frisco Mts.	19	8	11	11	11	38	9669	38.31	3
9	Mineral Mts.	34	12	22	24	25	11	9619	38.20	5
10	Pine Valley Mts.	46	18	28	79	39	10	10325	37.32	10
11	La Sal Mts.	64	25	39	314	28	42	13089	38.26	12
12	Abajo Mts.—Elk Ridge	42	22	20	368	38	70	11445	37.50	9
13	Henry Mts.	41	17	24	108	38	21	11615	38.07	7
14	Navajo Mtn.	49	22	27	13	62	58	10416	37.02	5
15	Wasatch-Uinta Mainland	80	33	47	—	—	—	13498	40.77	18

*N_1 = total number boreal species found; N_2 = number of these permanently resident; N_3 = no. summer residents; AR = total area above 7500 feet in square miles; WB = width of interisland lowland desert barrier, e.g., distance from closest boreal island, DM = distance from mainland; EHP = elevation of highest peak; LHP = latitude of highest peak; HDS = Habitat Diversity Score.

patchiness or some other aspect of the more extensive woodland on Navajo Mountain presumably accounts for the greatly increased number of species present. In these two instances, at least, total area is not as good a predictor of number of kinds of birds as is total forest woodland area with all the attendant attributes, whatever they may be.

From his study of boreal mammals on the mountaintops of the Great Basin ranges, Brown (1971) concluded that their diversity and distribution could not be explained in terms of an equilibrium between coloniza-

TABLE 2. Results of partial correlation analysis of island data. Upper number indicates the correlation coefficient; lower number is the level of significance. Meaning of symbols is the same as in Table 1.

	N_1	N_2	N_3	AR	WB	DM	EHP	LPH	HDS
	1.000								
N_1	.001								
	.933	1.000							
N_2	.001	.001							
	.970	.816	1.000						
N_3	.001	.001	.001						
	.442	.581	.313	1.000					
AR	.114	.029	.275	.001					
	.319	.428	.220	−.023	1.000				
WB	.267	.127	.449	.938	.001				
	.167	.169	.153	.329	−.018	1.000			
DM	.569	.564	.602	.251	.952	.001			
	.581	.673	.474	.771	.055	.128	1.000		
EHP	.029	.008	.087	.001	.851	.662	.001		
	.329	.145	.430	−.132	−.204	.305	−.016	1.000	
LHP	.250	.622	.125	.653	.485	.289	.956	.001	
	.867	.832	.824	.655	.091	.138	.714	.323	1.000
HDS	.001	.001	.001	.011	.757	.638	.004	.260	.001

TABLE 3. Summary of results from stepwise multiple regression analysis showing relationship of total number of bird species (the dependent variable) to independent variables. HDS = habitat diversity score; WB = width of interisland barrier; EHP = elevation of highest peak; AR = total area; DM = distance from mainland; LHP = latitude of highest peak.

Variable	Multiple R	R^2	R^2 Change	Simple r
Treatment A. EHP and AR excluded as independent variables				
HDS	.86693	.75156	.75156	.86693
WB	.89979	.80963	.05807	.31877
LHP	.90712	.82286	.01323	.32918
(constant)				
Treatment B. HDS excluded as an independent variable				
AR	.44173	.19512	.19512	.44173
LHP	.58987	.34795	.15283	.32918
WB	.72392	.52405	.17611	.31877
DM	.74207	.55067	.02661	.16689
(constant)				
Treatment C. All variables included in the analysis				
HDS	.86693	.75156	.75156	.86693
WB	.89979	.80963	.05807	.31877
AR	.91085	.82964	.02002	.44173
DM	.91693	.84076	.01111	.16689
(constant)	.91870	.84402	.00326	.58097
EHP				

tion and extinction. His interpretation was that boreal mammals reached all the islands during the Pleistocene and since then there have been extinctions but no colonizations. In his study of boreal birds, Johnson (1975) concluded that a similar nonequilibrium situation prevails for the permanent resident species, but for the summer residents the equilibrium theory of island species number does apply since species are excluded by habitat deficiencies rather than barriers.

Subspecies of Geographically Variable Species in Utah

An aspect of biogeography that is of primary interest to the systematist is the geographic distribution of different subspecies or races of geographically variable species. Twenty-three species present systematic problems in Utah. Of these, 7 are montane or boreal forms, 14 are valley or austral species, and 2 are wide-ranging types that extend from the valleys up to the mountaintops. Of the total, 14 are represented by 2 breeding races and 4 by 3 races, with possibly another in the last category. Another 4 species are represented by only one race in the state, but each has an intergrading population in some part of Utah that is transitional with another race in surrounding regions. The distribution of the races and populations in nine geographic regions in the state is indicated in Table 4 except for the Red Crossbill, about which a decision as to the number of races represented in Utah

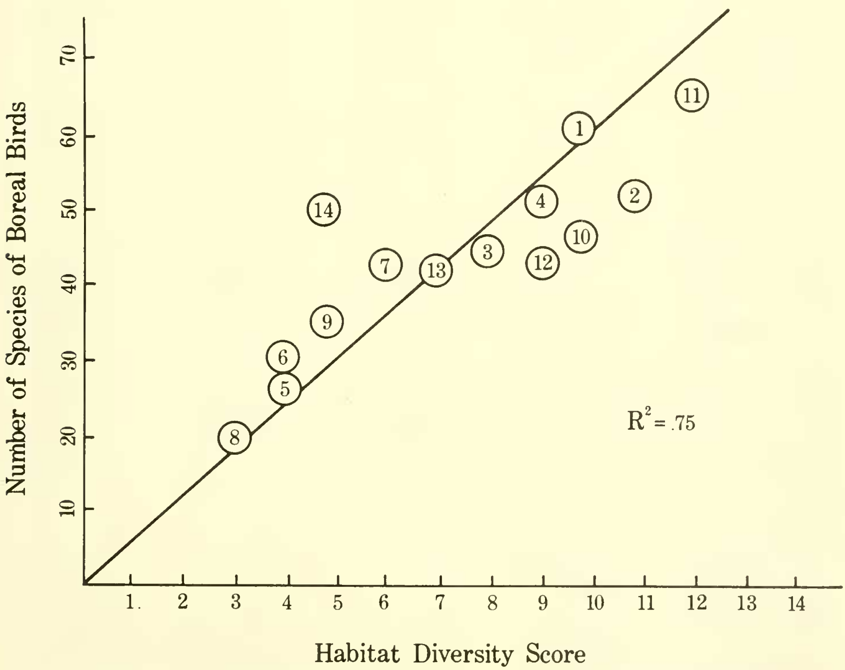

Fig. 2. Relationship between habitat diversity score (HDS) and total number of birds (N_1) occurring on boreal islands in Utah. Numbers of sample areas correspond to those used in Fig. 1 and Table 1. R^2 value shown is the adjusted value because of the small number of sample areas.

awaits the results of a pending systematic review by Allen Phillips. Areas of intergradation of varying extent occur between the races. Two instances of a minor barrier effect have been revealed. No uniform pattern of distribution prevails. Rather, there are several situations indicated whereby 2 or more species show racial changes in about the same general area. The picture of variation is more indicative of broad changes on a regional basis than of differentiation in isolated mountain ranges, as is often the case with more sedentary groups such as mammals.

One distributional pattern is where differences occur between populations in the west desert portion of northern Utah and those of the Wasatch and Uinta mountains. This is seen in the Dusky Grouse, Cliff Swallow, Mountain Chickadee, Brown Creeper, Scrub Jay, and Steller's Jay. Cliff Swallows represent an extreme case of gradual clinal variation, with only specimens from the ends of the cline in extreme western

Table 4: Subspecies of geographically variable birds or intermediate populations represented in various geographic areas in Utah.

	Raft River, Deep Creek Mountains	Stansbury, Oquirrh Mountains	House, Needle, Wah Wah Mountains	Pine Valley Mountains Virgin River Valley Beaver Dam Wash
Buteo jamaicensis Red-tailed Hawk	*calurus*	*calurus*	*calurus*	*calurus*
Dendragapus obscurus Blue Grouse	*oreinus*	*oreinus* > *obscurus*	–	*obscurus*
Otus asio Screech Owl	*inyoensis*	*inyoensis*	*inyoensis*	*inyoensis* > *yumanensis*
Bubo virginianus Great Horned Owl	*occidentalis*	*occidentalis*	*occidentalis*	*pallescens*
Chordeiles minor Common Nighthawk	*hesperis*	*hesperis*	*hesperis*	*henryi*
Picoides villosus Hairy Woodpecker	*leucothorectis* > *monticola*	*monticola*	*leucothorectis*	*leucothorectis*
Empidonax traillii Willow (Traill's) Flycatcher	*adastus*	*adastus*	*adastus* > *extimus*	*extimus*
Eremophila alpestris Horned Lark	*utahensis*	*utahensis*	*utahensis*	–
Petrochelidon pyrrhonota Cliff Swallow	*hypopolia*	*hypopolia* > *pyrrhonota*	*hypopolia* > *pyrrhonota*	*tachina*
Cyanocitta stelleri Steller's Jay	–	*macrolopha*	*macrolopha*	*macrolopha*
Aphelocoma coerulescens Scrub Jay	*nevadae*	*nevadae*	*nevadae*	*nevadae*
Parus atricapillus Black-capped Chickadee	*nevadensis*	*nevadensis*	*nevadensis*	*nevadensis*
Parus gambeli Mountain Chickadee	*inyoensis*	*inyoensis* > *wasatchensis*	*inyoensis* > *wasatchensis*	*inyoensis*
Certhia familiaris Brown Creeper	*leucosticta*	*leucosticta*	*leucosticta*	*leucosticta*
Catherpes mexicanus Canyon Wren	–	–	–	*conspersus*
Sialia mexicana Western Bluebird	–	–	–	–
Lanius ludovicianus Loggerhead Shrike	*gambeli*	*gambeli*	*gambeli*	*gambeli*
Geothlypis trichas Common Yellowthroat	*occidentalis*	*occidentalis*	*occidentalis*	*occidentalis* > *scirpicola*
Agelaius phoeniceus Red-winged Blackbird	*fortis* > *nevadensis*	*fortis*	*fortis*	*fortis* > *nevadensis*
Molothrus ater Brown-headed Cowbird	*artemisiae*	*artemisiae*	*artemisiae* > *obscurus*	*obscurus*
Carpodacus mexicanus House Finch	*solitudinus*	*solitudinus*	*solitudinus*	*solitudinus*
Melospiza melodia Song Sparrow	*montanus*	*montanus*	*montanus*	*fallax*

and eastern Utah sufficiently different to be assigned to separate races (see Behle 1976a). In two species more of a step cline is represented. In one of these, the Dusky Grouse, specimens from the Deep Creek Mountains near the Utah-Nevada border, are typical of the race *Dendragapus obscurus oreinus*. Those from the Oquirrh Mountains are closest to *oreinus* but show an approach to *obscurus*. In the Wasatch Mountains the grouse represent the race *obscurus*. A similar situation exists in the Mountain Chickadee. Those from the Deep Creek Mountains represent the race *Parus gambeli inyoensis*. Those from the Stansbury and Oquirrh mountains are closest to *inyoensis* but show an approach to *wasatchensis* which occurs in the Wasatch Mountains and thence east to the Uinta Mountains. In the Brown Creeper, representatives from all the west desert ranges represent the race *Certhia familiaris leucosticta*. Those from the Wasatch Mountains are a highly variable lot of intergrades but as a whole stand closest

Wasatch Mountains Wasatch Plateau	Pavant, Tushar Mountains	Aquarius, Paunsaugunt, Markagunt Plateaus	Uinta Mountains—Tavaputs Plateau	La Sal—Abajo Henry Mountains
calurus	*calurus*	*calurus*	*fuertesi*	—
obscurus	*obscurus*	*obscurus*	*obscurus*	*obscurus*
inyoensis	*inyoensis*	*inyoensis*	*inyoensis*	*inyoensis*
occidentalis	*occidentalis*	*occidentalis*	*occidentalis*	*pallescens*
hesperis	*hesperis*	*henryi*	*howelli*	*henryi*
monticola	*monticola*	*monticola* > *leucothorectis*	*monticola*	*luecothorectis*
adastus	*adastus* > *extimus*	*adastus* > *extimus*	*adastus*	*adastus* > *extimus*
utahensis	*leucolaema*	*leucolaema*	*leucolaema*	*leucolaema* *occidentalis*
hypopolia > *pyrrhonota*	*hypopolia* > *pyrrhonota*	*hypopolia* > *pyrrhonota*	*pyrrhonota* > *hypopolia*	*hypopolia* > *pyrrhonota*
macrolopha > *annectens*	*macrolopha*	*macrolopha*	*macrolopha*	*macrolopha*
woodhouseii > *nevadae*	*woodhouseii* > *nevadae*	*woodhouseii* > *nevadae*	*woodhouseii*	*woodhouseii*
nevadensis	*nevadensis*	*nevadensis*	*garrinus*	*garrinus*
wasatchensis	*wasatchensis*	*wasatchensis*	*wasatchensis*	*gambeli*
montana > *leucosticta*	*montana*	*montana*	*montana*	*montana*
conspersus > *griscus*	*conspersus*	*conspersus*	*conspersus*	*conspersus*
—	—	*bairdii*	*occidentalis*	*bairdii*
gambeli	*gambeli*	*gambeli*	*gambeli* > *excubitorides*	*gambeli* > *excubitorides*
occidentalis	*occidentalis*	*occidentalis*	*occidentalis*	*occidentalis*
fortis	*fortis*	*fortis*	*fortis*	*fortis*
artemisiae	*artemisiae*	*artemisiae*	*artemisiae*	*artemisiae*
solitudinus > *frontalis*	*solitudinus* > *frontalis*	*solitudinus* > *frontalis*	*solitudinus* > *frontalis*	*frontalis*
montanus	*montanus*	*montanus*	*montanus*	*montanus*

to the race *montana*. The Steller's Jays of the west desert ranges including the Oquirrh Mountains are typical of the race *Cyanocitta stelleri macrolopha*, while those from the Wasatch Mountains constitute an intergrading population between *macrolopha* and *annectens*, a northern race. The Scrub Jays of the Oquirrh Mountains and other west desert ranges are typical of the race *Aphelecora caerulescens nevadae*, but those from the Wasatch are intergrades between *nevadae* and *woodhouseii*, closest to the latter. Thus in these several species a break occurs along the west escarpment of the Wasatch Mountains dividing west desert races from intergrading populations in the Wasatch Mountains and eastward. The Jordan Valley between the Oquirrh and Wasatch Mountains, only about 25 miles across, thus seems to act as a weak barrier for the montane forms.

The second pattern is for the break along a west-east cline to occur farther east between the Wasatch and Uinta mountains. Here there is not even a valley to serve as the line of demarcation. This situation is seen in the Red-tailed Hawk and Black-capped Chickadee. For the hawk, the population in the Wasatch and all of western Utah represents the race *Buteo jamaicensis calurus*, while those from the Uinta Basin and Tavaputs Plateau region are closest to *fuertesi*, a race which extends southeast into Texas. The Black-capped Chickadee of the Oquirrh and Wasatch ranges represents the race *Parus atricapillus nevadensis*. By the time the Uinta Basin is reached the population represents *garrinus*.

The third pattern is for a race or population to be represented in northern Utah and a different one in the southern part of the state. Exemplifying this are the Steller's Jay, Hairy Woodpecker, and Great Horned Owl. As previously noted, the Steller's Jays from the Wasatch Mountains represent an intergrading population between the races *annectens* and *macrolopha*, closest to the latter. In southern Idaho the jays are closest to *annectens*. South of Mount Nebo at the southern end of the Wasatch Mountains, the jays are typical of *macrolopha*. In the case of the Hairy Woodpecker the break occurs south of the Aquarius, Paunsaugunt, and Markagunt plateaus. This is farther south than the transition area for the Steller's Jays. An unexpected distributional feature of the Hairy Woodpecker is that the southern race *Picoides villosus leucothorectis* extends farther north in the isolated mountain ranges of the Great Basin in western Utah than it does in the plateaus and mountains of central Utah. This suggests that the propagules for the west desert ranges came from the southeast rather than directly west from the Wasatch, a situation similar to that of the Three-toed Woodpecker (Johnson 1975: 548). Whatever the direction of spread, *leucothorectis* and *monticola* seem to have met in the Snake and Deep Creek ranges where an intergrading population occurs. In contrast, a sharp break in the distribution of the two subspecies occurs between the Tushar and Mineral mountains in southwestern Utah. The population of the Tushar Mountains is *monticola* while that of the Mineral Range about 25 miles to the west with Beaver Valley between is typical *leucothorectis*. In the case of the Horned Owls, the race extending across southern Utah is *Bubo virginianus pallescens* but its range swings north in eastern Utah to include the La Sal Mountain-Moab region.

The fourth situation is found in extreme southwestern Utah along the Virgin River Valley, where, in addition to the numerous indicator species of the Mojave Desert avifauna previously discussed, there are differences at the subspecies level for several kinds of birds. In three geographically variable species there are races that do not occur elsewhere in the state. These are a subspecies of Cliff Swallow (*Petrochelidon pyrrhonota tachina*), a race of Brown Cowbird (*Molothrus ater obscurus*), and a race of Song sparrow *Zonotrichia melodia fallax*). These three races are of southern origin. In four other species, the populations are intergradational toward southern races. This is the case for the Screech Owl, where the population is *Otus asio inyoensis* toward *yumanensis*. The Gilded Flicker (formerly *Colaptes chrysoides* but now considered to be *C. auratus chrysoides*) has been observed in Beaver Dam Wash in Utah, and one specimen has been obtained that is intermediate between that race and the Red-shafted Flicker (*C. a. cafer*). In the Rough-winged Swallow, the population is *Stelgidopteryx ruficollis serripennis* toward *psammochroa*. In the Yellow-throat, the population is *Geothlypis trichas occidentalis* toward *scirpicola*. Yet another intergrading population occurs in the region in the case of the Red-winged Blackbird, but the race with which intergradation occurs is a western race. The population is *Agelaius phoeniceus fortis* toward *nevadensis*.

A fifth distributional pattern shows a different population in the Red Rock country of southeastern Utah as compared to the rest of the state. This is seen in the Nighthawks and Horned Larks. For the former, the race in southeastern Utah is *Chordeiles minor henryi* as opposed to *howelli* to the north in the Uinta Basin and *hesperis* in western Utah. For the Horned Larks there is an intergrading population between the race *Eremophila alpestris leucolaema* and *occidentalis* in southeastern Utah that is closest to *leucolaema*.

Finally, a situation occurs in the Horned Larks that is unlike the racial distribution of any other geographically variable species in the state. One race, *leucolaema*, occurs in subalpine meadows in the plateaus of central Utah and in alpine tundra of the Tushar Mountains, while a different race, *utahensis*, occupies the desert floor of the valleys below. The high elevation race is the same as the lowland race of the Uinta Basin in northeastern Utah. This same phenomenon of two races at different altitudes in the same general region is found in the Sierra Nevada (see Behle 1942), where the race *sierrae* occurs in montane meadows as opposed to different races in the lowland valleys both east and west of the mountains. In contrast, in the Raft River Mountains of northwestern Utah, Horned Larks taken from the top of the mountain at 9500 feet represent the same race as in the lowlands, namely *utahensis;* and, in the Colorado Rockies, the race *leucolaema* ranges from the valleys up to the Arctic tundra at over 11,000 feet.

Clinal Variation

Clines are essentially a phenomenon of geographic variation but they are also part of the picture of biogeography inasmuch as they would not be evident if samples were not present from many geographic areas. Clinal variation is manifest in the characters of many kinds of birds in the Great Basin and Utah. Occasionally similar clines appear in unrelated species, which suggests that some common environmental influence is exerting a selective influence. Clines in some instances extend in a north-south direction, while in others they extend from east to west or northeast to southwest. Phillips (1958) mentions the Song Sparrow (*Zonotrichia melodia*) in the Great Basin as an example where two clines cross perpendicularly. One cline toward longer wings and darker color extends northward while another toward short wings, large bill, and heavy breast-spotting proceeds westward. In connection with his work on the birds of Nevada, Linsdale (1938: 175) itemized the changes observed for several variable species, then generalized that for many birds there is a decrease in size toward the south. The largest individuals occur in the northeastern corner of the state. The bill becomes shorter and stubbier toward the east and smaller toward the south. The wings and tail are generally longer toward the east. General coloration becomes paler and grayer toward the east and sometimes brighter and darker in the vicinity of the Colorado River.

In Utah, clines are most evident in size characters. The usual pattern is for birds in the northern part of the state to be of larger size than those in the southern part, with a smooth gradient occurring the length of the state. The gradient in Utah is usually a portion of a more extensive cline extending throughout western North America. A recent study that I made of the White-throated Swift (Behle 1973) revealed clinal variation nicely. Measurements of populations from Montana south to Arizona were analyzed. Clinal variation was most apparent in wing length, which is regarded in ornithological systematics as a good indicator of overall size. Clinal variation was less evident in tail length and virtually nonexistent in bill and tarsal lengths. For wing length, the means for the several populations measured showed a gradual transition from 143.2 mm in the Montana sample to 136.5 in the Arizona-New Mexico sample, a difference of 6.7 mm. While there was a general decrease in wing length from north to south in Utah samples, a mosaic pattern of variation was shown in the several semi-isolated populations represented. For example specimens from the Raft River Mountains in northwestern Utah have the longest wings in the state (average wing length 146.0 mm). They are larger than those from central northern Utah, northeastern Utah, or Colorado and are closest to the Montana population in size. Swifts from the Beaver Dam Wash in extreme southwestern Utah have the shortest wing length (wing 134.2). They are smaller than samples from central southern and southeastern Utah and are even smaller than the Arizona-New Mexico sample. These extreme Utah populations differ in average wing length by 11.8 mm, which is greater than that between Montana and Arizona-New Mexico birds (6.7 mm). The circumstance that northern swifts have longer wings than do southern swifts may be correlated with the behavioral feature that northern individuals migrate during the winter from their breeding areas while those in the southern part of their range are sedentary. Another case of north-south clinal variation in size is seen in the Cliff Swallows in western North America (Behle 1976a). Clinal variation in size in Utah has become apparent from our studies of the Great Horned Owls and Hairy Woodpeckers (unpublished data).

Clines are also evident in Utah birds in color characters. A west-east gradient occurs in several species in northern Utah whereby paler-colored birds occur in the desert Great Basin portion of the state, with a transition eastward to darker birds in the Wasatch and Uinta mountains. Such clines are most evident in dorsal coloration. Species showing this phenomenon are the Dusky Grouse, Screech Owl, Common Nighthawk, Cliff Swallow, Horned Lark, Scrub Jay, Mountain Chickadee, and Creeper. Of the lot, the phenomenon seems to be most pronounced in the Dusky Grouse. Representatives are pale and gray in the ranges of eastern Nevada and in the Deep Creek Mountains of western Utah. In the Oquirrh Mountains they start to be slightly darker, showing more brown. The darkening is accentuated in the Wasatch Mountains and continues to a still greater degree in the Uinta Mountains and eastward into Colorado. In general, east-west clinal variation in Utah is the reverse of that for Nevada, since the birds become paler and grayer in the western part of the state, where the Great Basin occurs. Clinal variation in color from darker birds in the north to lighter birds in the south shows up in a few birds such as the Steller's Jay. In Utah, as in Nevada, brighter coloration occurs in some species in the valley of the Virgin River. Examples showing this are Yellow-throats and Song Sparrows.

Secondary Contact of Species in the Intermountain Region

In recent years several studies have been made of secondary contact of pairs of closely related species or subspecies of birds in North America (see Selander 1965: 536, for a listing of kinds and sources of information). For most cases, the area of contact is the Great Plains, but in four instances the phenomenon shows up in Utah. Three of these involve eastern and western kinds hybridizing. The fourth involves a northern and a southern species meeting. For two of the four the contact has probably been brought about during the past few decades; the other two are of longer duration. The first case pertains to the Indigo Bunting (*Passerina cyanea*, a species that originally occurred only in eastern North America), and the Lazuli Bunting (*P. amoena*), a western species. Apparently the planting of trees and shrubs in cities and parks across the plains states bridged the former grasslands hiatus separating the two species, and a highway was thus provided for dispersal of the Indigo Bunting westward into the range of the Lazuli Bunting. Historical records suggest that the Indigo Bunting arrived in Utah about 40 years ago. That hybridization of the two species has occurred is indicated by two intermediate specimens. One, in the Cornell University collection, was taken near Ogden, Weber County, Utah, on 12 August 1945 (Sibley and Short 1959: 447). The other is in the University of Utah collection and was taken along Minnie Maud Creek, 2 miles east of Nutter's Ranch Duchesne County, Utah, on 30 June 1966. The Indigo Bunting is now fairly common in southern Utah, where it exists sympatrically with the Lazuli Bunting. Whitmore (1975) has recently discussed the interspecific behavioral competition now in evidence in this region between the two species.

The second instance of recently established contact in Utah pertains to two kinds of oriole, the Baltimore Oriole, formerly called *Icterus galbula*, which is an eastern type, and the Bullock's Oriole, formerly designated as *I. bullockii*, a common western kind. Worthen (1973) reported an example of the Baltimore Oriole taken 2 miles south of Milford, Beaver County, Utah, on 27 June 1964. It was one of a series of several orioles obtained at this location. Although in worn plumage, the specimen represents a "pure" first-year male. While this particular specimen shows no tendency toward the Bullock's Oriole, some others in the series do show evidences of hybridization. Sibley and Short (1964) have shown that hybridization in the two orioles is now common throughout the Great Plains. As a result, the two orioles are presently considered as races of one species, e.g., *I. g. galbula* and *I. g. bullockii*.

The third case of hybridization in Utah pertains to flickers. There are three types of flickers in North America: the Yellow-shafted Flicker, essentially an eastern bird formerly designated as *Colaptes auratus;* the Red-shafted Flicker of the west, formerly called *C. cafer;* and the Gilded Flicker of the southwest and lower California, formerly called *C. chrysoides*. The Yellow-shafted and Red-shafted forms for over 100 years have been known to hybridize in a broad montane belt in western North America extending from British Columbia southward throughout the Rocky Mountain region. Short (1965) interprets the picture of speciation as follows. He postulates a geographic separation of the ancestral *auratus-cafer* population during the Illinois glacial age or earlier. The separation continued during subsequent periods of glaciation (except for possible hybridization between the two differentiated stocks during interglacial periods). With the waning of the last major advance of the Wisconsin period of glaciation, the eastern Yellow-shafted Flicker, *auratus*, was able to expand its range westward and northwestward into British Columbia. In contrast, the Red-shafted Flicker, *cafer*, remained restricted to the area south of the glaciers in the western United States. Eventually the two populations made contact and hybridized along the length of the Rockies. Utah is west and south of the main zone of introgression and Short scarcely mentions the area in his discussion, but there is evidence of much crossing taking place in Utah. A recent study by Rich (1967) of 137 specimens in the University of Utah collection revealed that 85 are "pure" *cafer*, 4 are "pure" *auratus*, and 48 are intermediates. This is a surprisingly large number of intergrades with so few *auratus* seemingly present. It suggests that there is little or no selective pressure against the characters produced by *auratus* genes. The greatest flow of *auratus* genes into the *cafer* population pool in Utah appears to be occurring in northwestern Utah, as indicated by the highest incidence of intermediates. In contrast, there are fewer intermediates from eastern Utah, suggesting that the east-west gradient from the Great Plains area is not of great significance in Utah. In other words, the Yellow-shafted Flickers in Utah have seemingly come mostly from the northwest rather than the east. Intermediates occur throughout the Great Basin mountain ranges.

Short (1965) conceives of all the North American flickers belonging to a single species, *Colaptes auratus*, and, following his lead, the Yellow-shafted Flicker is now known as *C. a. auratus*, the Red-shafted Flicker is *C. a. cafer*, and the Gilded Flicker is *C. a. chrysoides*. The latter apparently hybridizes with the Red-shafted Flicker in extreme northwestern Arizona and southwestern Utah; Wauer and Russell (1967) report a specimen taken at the Terry Ranch in Beaver Dam Wash, Washington County, on 28 April 1965 as being a hybrid of *chrysoides* × *cafer* derivation.

The last case of secondary contact in Utah involves two species of junco that come together in extreme northern Utah, with a relatively restricted zone of hybridization extending in an east-west direction across the state. One population is a northern form, a race of the Dark-eyed (Oregon) Junco (*Junco hyemalis mearnsi*). The other is a southern form, the Gray-headed Junco (*J. caniceps caniceps*). The contact of these two kinds was originally detected by Miller (1941: 200). At a locality 10 miles east of Kamas, all examples that he collected were pure *caniceps*. There was a shift in frequency of characters of *J. h. mearnsi* northward indicated by specimens from 20 miles north of Kamas, in the Uinta Mountains, then in succession Woodruff, Randolph, and Garden City, until nearly pure populations of *mearnsi* were found near the Utah-Idaho border. Since then breeding hybrid juncos have been taken in the Wasatch Mountains east of Salt Lake City and in the Uinta Mountains. Hybrids extend westward in northern Utah to the Raft River Mountains and beyond into northeastern Nevada.

Centers of Differentiation in the Great Basin

On a previous occasion (Behle 1963), I studied the distribution of the races of 50 geographically variable species of birds whose ranges include or impinge upon the Great Basin and its flanking regions. The results showed that the Great Basin is not in itself one large center of differentiation. Instead, several distribution areas were revealed that either occur in portions of the Great Basin or are situated in nearby surrounding regions. The areas were designated as the Warner Region, Sierra Nevada, Western Great Basin, Eastern Great Basin, Rocky Mountains, Northern Idaho, Inyo Region, Mojave Desert, Colorado Desert, and Navajo Country. The races of the geographically variable species occurring in each of the 10 distribution zones were listed. Since many species occupied each area, it was the different combinations of races along with common transition zones or areas of intergradation between races that served to characterize and delimit the several areas. No one species showed conformance in the distribution of its races with the various distribution areas outlined, although the horned lark approached this in slight degree. In only a few instances were races endemic in any one area. The Great Basin is too diversified in terms of environmental factors to have influenced in some common way all the geographically variable birds that are found in the region. The differentiation and distribution of the races is presumably correlated largely with localized different environments, but, in addition, barrier effects and individual histories of the various kinds of birds in terms of their point of origin, dispersal, and dependency on particular plant associations have played a role.

There are indications of three centers of differentiation in the Great Basin region, one in the eastern part, and two in the western portion. The latter two have been evaluated by Miller (1941). One is the White Mountain area of eastern California in the southwestern portion of the Great Basin. The other is the Warner Mountain-Warner Valley region of southern Oregon and northeastern California in the northwestern portion of the Great Basin. More recently Johnson (1970) presented additional data for the avifauna of the Warner Mountains and has reevaluated the affinities of the boreal elements. He gives different results than I presented (Behle 1963). The center of differentiation in the eastern part of the Great Basin rests on four races that have fairly common, though not identical, ranges. Three of these were described in the course of our fieldwork at the University of Utah, namely a race of Dusky Grouse (*Dendragapus obscurus oreinus*), a race of Horned Lark (*Eremophila alpestris utahensis*), and a race of Fox Sparrow (*Passerella iliaca swarthi*). The fourth is a race of Black-capped Chickadee (*Parus atricapillus nevadensis*) described by Linsdale of the University of California.

Theoretical Historical Aspects of Distribution of Birds in the Great Basin

To my knowledge, no direct evidence has been detected of the influence of Pleistocene or Holocene climates on the distribution of birds in the Great Basin or Intermountain Region. Still, some inferences can be drawn. Resident birds present in the region today are closely associated in their occurrence with particular biotic communities, especially the plant components. Since climatic change has resulted in alteration of community types, the avian associates have almost certainly been affected too, either being forced out of areas where the plant habitat has disappeared or invading new areas as their requisite habitat has become established. Dispersal resulting from population pressure has also resulted in extensions of ranges. In some instances former allopatric species have become sympatric, as in the cases of the flickers and buntings. With contractions of ranges, former sympatric species conceivably have become allopatric. Such movements would be in the nature of long-term adjustments.

Of particular interest in this connection is the present-day discontinuous distribution of the coniferous forest on the mountaintops of the Great Basin and the attendant boreal species of birds. Johnson (1975: 556) has noted the two theories that have been offered to account for this. One proposes that during the Pleistocene cold climates prevailed with relatively more moisture and less evaporation than in the region today. These conditions induced the formation of glaciers in the mountains and the pluvial lakes Bonneville, Lahonton, and a host of lesser lakes on the floor of the Great Basin. At the same time, the coniferous forest presumably extended altitudinally down into the valleys, bordering on the lakes, and became distributed more or less continuously throughout the Great Basin. Boreal species of birds presumably accompanied the coniferous forest and also occurred more or less continuously at lowland elevations. Subsequent climatic change to the warmer and drier conditions of today resulted in melting of the glaciers, disappearance or diminution of the lakes, and retreat of the coniferous forest up into the mountains. The boreal birds presumably were also forced to move up into the mountains, where they occur as breeders today. Martin and Mehringer (1965) have mobilized the evidence from pollen studies in support of such climatic changes. In accord with this line of reasoning such avian species as the northern Three-toed Woodpecker, Water Pipit, and

Black Rosy Finch were presumably formerly much more widespread and abundant but have subsequently been confined to the mountaintops where Hudsonian zone or alpine-arctic conditions prevail. Concurrently the lowland valleys were invaded by lowland species from surrounding regions, species adapted to the warmer, xeric conditions that have come to prevail there.

The second point of view is that the montane pockets of boreal forest and attendant faunas have come about through dispersal over long distances from parental stocks such as those in the Sierra Nevada and Rocky mountains. Some evidence pertaining to the vegetation to support this interpretation has been presented by Wells and Berger (1967) and Critchfield and Allenbaugh (1967), and Johnson (1975) has noted the probable role of certain species of boreal birds such as the Band-tailed Pigeon, Pinyon Jay, and Clark's Nutcracker in long-distance colonization through transporting and/or burying seeds of conifers. In accordance with this theory, the Three-toed Woodpecker, Water Pipit, and Black Rosy Finch have extended their ranges westward from the Rocky Mountain continental area only to certain boreal islands in the eastern part of the Great Basin. Present indications are that the Rosy Finch has progressed the farthest, being known from the Jarbidge Mountains, the Ruby Mountains, and the Wheeler Peak area of the Snake Range in eastern Nevada. The Water Pipit stops at the Deep Creek Range in extreme western Utah. The Northern Three-toed Woodpecker is known from the Snake Range. However, I suspect that if more collecting were done, all three species would be found at Wheeler Peak and the Ruby Mountains in Nevada. I favor the relict mountaintop theory as Brown (1971) does for mammals. As Johnson notes, these two hypotheses are not mutually exclusive. Both processes could have occurred in the past. Extensions of range are occurring at present, as indicated by the historic record for certain species. The diversity of distribution patterns that have been noted for Utah leads to the inference that each species has had its own particular distributional history determined by its habitat requirements and the habitat changes experienced.

Management Implications

Birds come into the picture of natural resource management in the Great Basin in several ways. In connection with environmental impact studies, special consideration is being given to threatened and endangered species such as the Bald Eagle, Peregrine Falcon, and Osprey. All of these occur in the Great Basin. Indeed, studies of raptors by Brigham Young University biologists have revealed high populations for many species in remote areas of the Great Basin. Even subspecies are important in terms of endangered species, because it is the southern race of Bald Eagle and the southern race of Peregrine Falcon that are endangered. Another area where subspecies are important in management pertains to the introduction of exotic game species. If more should be introduced (and there are serious objections to the practice) stock should be selected representing races whose native habitat is most nearly like that where the introduction is to be made. Another point is that populations at type localities, such as the Dusky Grouse (which is a game species) from the Deep Creek Mountains, should be protected. Regional avifaunistic reports, such technical papers as descriptions of new forms and systematic revisions, and symposia such as the present one, especially the published proceedings, constitute valuable resource material for those charged with making evaluations. They provide baseline data to compare against in future years to establish long-term changes.

In the 130 years since settlement of the Great Basin and other parts of the Intermountain West, many well known changes have occurred in the vegetation as pointed out by Cottam (1947) and others. Concomitant changes have occurred in the bird life. For example, as the grassland was essentially extirpated from Utah through overutilization, the habitat for the Grasshopper Sparrow and Sharp-tailed Grouse was removed, the result being the near extermination of these kinds of birds in the region today. As pertains to the grouse, certain protected areas containing the little remaining requisite habitat are needed for its survival. One such tract is east of Wellsville, Cache County, Utah. As more and more sagebrush is removed for land cultivation, Sage Grouse and other sage-inhabiting species are being affected. The Conservation Committee of the Wilson Ornithological Society (see Braun et al. 1976) has recently reported on the extent of alteration of this community and attendant deleterious effects on the associated bird life. Chaining out of junipers and pinyon pine in the Great Basin is of less consequence in terms of the bird life because the extent of the habitat is so vast. Nevertheless, I feel that some typical areas should remain undisturbed to serve as study areas. They should be large enough to preserve habitat diversity and maintain spatial relations intact. Yet extensive areas of continuous forest may not be as effective in preserving communities and species as would numerous, smaller, diversified, irregular areas. A large, essentially undisturbed and diversified area is the Wheeler Peak region in the Snake Range in eastern Nevada. At one time the area was proposed for a Great Basin natural park. I would like to see this area so designated. This would afford some measure of protection. The Lehman Cave National Monument has already been established there. The Bureau of Land Management is, I believe, considering the designation of the Deep Creek Mountain in western Utah as a quasi-primitive area. A complication is that part of that range is Indian reservation. The Beaver Dam Wash area of extreme southwestern Utah is unique in its flora and fauna and needs protection—especially from collectors.

Regarding such theoretical considerations as the application of island biogeography theory to conservation practice as has been advocated in the design of wildlife refuges, Simberloff and Abele (1976) express the opinion that the application of the general principle is premature at the present time. They feel that, in this particular instance, broad generalizations have been based on limited and insufficiently validated theory and on field studies of taxa which may be idiosyncratic. The implication is that much more research is needed. I suggest that the boreal islands of the Great Basin constitute propitious areas for further avian research as a sequel to Johnson's and my work.

Summary and Conclusions

Although there are no endemic species of birds in the Great Basin region of western North America, nevertheless a distinctive avifauna exists there by virtue of a different combination of birds as well as the presence of many species associated with sagebrush and the pinyon-juniper forest. Physiographic boundaries determine the limits of the Great Basin avifauna on the west and east, while on the south there is a sharp junction zone with the Mojave Desert avifauna that occurs in southern Nevada and in extreme southwestern Utah. To the north there is a gradual blending with the avifauna of the Palouse prairie and the northern montane woodland. About 30 kinds of distinctive birds that occur in the California-Pacific Coast-Sierra Nevada region are not known to occur in the Great Basin, suggesting that relatively little eastward spread has occurred. In contrast, seven Rocky Mountain species reach their western limits within the Great Basin. Some of the latter group, namely the Yellow-shafted Flicker, Baltimore Oriole, and Indigo Bunting, are recent arrivals and introgression has occurred with western congeners. Instability of present-day ranges for many species of birds is further indicated by the finding in recent years of several other kinds, mostly in southwestern Utah, that are new to the state list.

Ten northern species reach their southern limits in at least part of their ranges in the Great Basin. A zone of hybridization between a race of the northern Dark-eyed Junco (*J. h. mearnsi*) and the southern Gray-headed Junco (*J. c. caniceps*) occurs across northern Utah and northeastern Nevada. Sixteen southern species reach their northern limits in the Great Basin, while an additional 25 species stop at a distinct Great Basin—Mojave Desert junction zone in southern Nevada and extreme southwestern Utah. Three avifaunas are represented in the Great Basin region today, namely the Rocky Mountain, Great Basin, and Mojave Desert.

Montane species, which are mostly associated with the coniferous forest, are discontinuously distributed in boreal islands on the tops of isolated mountain ranges in the general region. An analysis of the avifaunas of 14 such islands in western and southeastern Utah, as compared with that of the Rocky Mountain continent in central and northern Utah, shows a close correlation between the number of species present and habitat diversity. A slight, negative correlation shows up for permanent residents with distance from the continent. The results are similar to those of Johnson (1975) for a different set of islands mostly located in Nevada.

An analysis of the distribution of races of 22 species in Utah represented by more than one race in the state reveals a variety of patterns. For several a break occurs along the Wasatch Front on the east side of the Great Basin between a west desert race and either an eastern montane race or an intergrading population toward a different race in eastern Utah. In a few others, the break is farther east between the Wasatch and Uinta mountains. Another situation is for there to be one race in northern Utah and a different race in the southern part of the state. In three species, there are different races or populations in southeastern Utah; but southwestern Utah is the most distinctive transitional area where, in three species, different races are represented and in five others intergradational populations occur. For the Horned Lark, one race occurs in subalpine meadows in central Utah, and a different race is a summer resident in the desert region at the base of the mountains. In some species intergrading populations occur over broad areas; in others the phenomenon is confined to a narrow zone.

A center of differentiation occurs in western Utah in the eastern portion of the Great Basin where four races of geographically variable birds have ranges that somewhat coincide. This is similar to the White Mountain and Warner Mountain centers in the western portion of the Great Basin. Clinal variation occurs in many species, involving both size and color characters. Some clines run north and south and others run east and west. Some are gradual; others are step clines. Past climatic change has doubtless influenced the distribution of species and avifaunas in the region. It is inferred that during cold intervals of the Quaternary boreal birds occurred in lowland valleys, but with a warming trend they have retreated to the mountaintops, where they are found today. This would account for the current distribution of the Water Pipit and Black Rosy Finch, although the possibility exists of a westward spread of these species from the Rocky Mountains.

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Appendix

Occurrence of boreal birds on montane islands and portion of Rocky Mountain Continent in Utah.

	Raft River Mts. (Behle 1958)	Deep Creek Mts. (Behle 1955)	Stansbury Mts. (Porter, Bushman, and Behle MS)	Oquirrh Mts. (Blanchard 1973)	House Range (Worthen 1968)	Needle Range (Worthen 1968)	Wah Wah Mts. (Worthen 1968)	Frisco Mts. (Worthen 1968)	Mineral Mts. (Worthen 1968)	Pine Valley Mts. (Behle 1943)	La Sal Mts. (Behle 1960)	Abajo Mts.–Elk Ridge (Behle 1960)	Henry Mts. (Behle 1960)	Navajo Mtn. (Benson 1935; Woodbury *et al.* 1945)	Wasatch, Uinta, High Plateaus, Tushar Mts. Continent
°Goshawk (*Accipiter gentilis*)	X	X		X		X	X					X	X	X	X
°Sharp-shinned Hawk (*Accipiter striatus*)	X	X	X	X	X		X			X	X	X	X	X	X
°Cooper's Hawk (*Accipiter cooperii*)	X	X	X	X			X		X		X	X		X	X
°Red-tailed Hawk (*Buteo jamaicensis*)	X	X	X	X	X		X	X	X	X	X	X		X	X
°Golden Eagle (*Aquila chrysaetos*)	X	X	X	X	X		X			X	X			X	X
°American Kestrel (*Falco sparverius*)	X	X	X	X							X	X	X	X	X
°Dusky Grouse (*Dendragapus obscurus*)	X	X	X	X						X	X	X	X		X
°Ruffed Grouse (*Bonasa umbellus*)	X														X
°Band-tailed Pigeon (*Columba fasciata*)										X	X	X	X	X	X
°Flammulated Owl (*Otus flammeolus*)			X									X		X	X
°Great Horned Owl (*Bubo virginianus*)	X	X		X					X	X	X			X	X
°Pygmy Owl (*Glaucidium gnoma*)															X
°Spotted Owl (*Strix occidentalis*)														X	X
°Long-eared Owl (*Asio otus*)		X		X											X
°Saw-whet Owl (*Aegolius acadicus*)	X		X	X											X
White-throated Swift (*Aeronautes saxatalis*)	X	X			X		X	X	X	X	X	X	X	X	X

Species ° = Permanent residents. Others are summer residents.

Black-chinned Hummingbird (*Archilochus alexandri*)	X			X						X				X	X
Broad-tailed Hummingbird (*Selasphorus platycercus*)	X	X	X	X	X		X		X	X	X		X	X	X
Calliope Hummingbird (*Stellula calliope*)															X
°Common Flicker (*Colaptes auratus*)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
°Pileated Woodpecker (*Dryocopus pileatus*)															X
°Yellow-bellied Sapsucker (*Sphyrapicus varius*)	X					X	X		X	X	X	X	X	X	X
°Williamson's Sapsucker (*Sphyrapicus thyroideus*)												X			X
°Hairy Woodpecker (*Picoides villosus*)	X	X	X	X		X	X	X	X	X	X	X	X	X	X
°Downy Woodpecker (*Picoides pubescens*)	X	X	X	X							X				X
°Northern Three-toed Woodpecker (*Picoides tridactylus*)										X	X	X	X		X
Hammond's Flycatcher (*Empidonax hammondii*)	X	X	X				X			X	X	X	X		X
Dusky Flycatcher (*Empidonax oberholseri*)	X	X	X	X	X	X	X		X		X	X	X		X
Western Flycatcher (*Empidonax difficilis*)	X	X	X	X		X			X		X			X	X
Western Wood Peewee (*Contopus sordidulus*)	X	X	X	X					X	X	X	X	X	X	X
Olive-sided Flycatcher (*Contopus borealis*)	X	X					X	X			X		X	X	X
Horned Lark (*Eremophila alpestris*)	X												X		X
Violet-green Swallow (*Tachycineta thalassina*)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Tree Swallow (*Tachycineta bicolor*)	X			X						X	X			X	X
Purple Martin (*Progne subis*)															X
°Gray Jay (*Perisoreus canadensis*)											X	X			X
°Steller's Jay (*Cyanocitta stelleri*)	X	X	X	X			X		X	X	X	X	X	X	X
°Clark's Nutcracker (*Nucifraga columbiana*)	X	X	X	X	X	X	X	X		X	X	X	X	X	X
°Black-capped Chickadee (*Parus atricapillus*)	X	X	X	X					X		X				X
°Mountain Chickadee (*Parus gambeli*)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
°White-breasted Nuthatch (*Sitta carolinensis*)	X	X								X	X	X	X	X	X
°Red-breasted Nuthatch (*Sitta canadensis*)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
°Pygmy Nuthatch (*Sitta pygmaea*)							X			X	X	X	X	X	X
°Brown Creeper (*Certhia familiaris*)	X	X	X	X		X			X	X	X	X		X	X
House Wren (*Troglodytes aedon*)	X	X	X	X	X	X	X		X	X	X	X	X	X	X

Rock Wren (*Salpinctes obsoletus*)	X	X	X	X	X	X	X			X	X	X	X	X	X
American Robin (*Turdus migratorius*)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hermit Thrush (*Catharus guttatus*)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Swainson's Thrush (*Catharus ustulatus*)	X			X							X				X
Veery (*Catharus fuscescens*)	X														X
Western Bluebird (*Sialia mexicana*)											X			X	X
Mountain Bluebird (*Sialia currucoides*)	X	X	X	X	X	X	X	X	X	X	X	X	X		X
Townsend's Solitaire (*Myadestes townsendi*)	X	X		X		X	X		X	X	X	X			X
Golden-crowned Kinglet (*Regulus satrapa*)	X	X		X							X			X	X
Ruby-crowned Kinglet (*Regulus calendula*)	X	X	X	X	X	X	X	X	X	X	X	X		X	X
Water Pipit (*Anthus spinoletta*)		X									X				X
Solitary Vireo (*Vireo solitarius*)	X	X	X	X			X		X	X	X			X	X
Warling Vireo (*Vireo gilvus*)	X	X	X	X	X	X	X		X	X	X		X	X	X
Orange-crowned Warbler (*Vermivora celata*)	X	X	X	X			X				X				X
Virginia's Warbler (*Vermivora virginiae*)	X	X	X	X		X	X		X	X	X		X	X	X
Yellow-rumped Warbler (*Dendroica coronata*)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Grace's Warbler (*Dendroica graciae*)														X	X
MacGillivray's Warbler (*Geothlypis tolmiei*)	X	X	X	X		X	X			X	X	X	X	X	X
Wilson's Warbler (*Wilsonia pusilla*)															X
Western Tanager (*Piranga ludoviciana*)	X	X	X	X		X	X		X	X	X	X	X	X	X
Black-headed Grosbeak (*Pheucticus melanocephalus*)	X	X	X	X			X		X	X	X	X	X	X	X
Cassin's Finch (*Carpodacus cassinii*)	X	X	X	X	X	X	X	X		X	X	X		X	X
°Pine Grosbeak (*Pinicola enucleator*)											X				X
Black Rosy Finch (*Leucosticte atrata*)	X										X				X
°Pine Siskin (*Carduelis pinus*)	X	X	X	X	X	X	X	X	X	X	X		X	X	X
°Red Crossbill (*Loxia curvirostra*)					X	X	X	X			X	X	X	X	X
Green-tailed Towhee (*Pipilo chlorura*)	X	X	X	X	X	X	X		X	X	X		X		X
Rufous-sided Towhee (*Pipilo erythrophthalmus*)			X	X	X		X		X	X	X		X	X	X
Vesper Sparrow (*Pooecetes gramineus*)	X	X								X	X		X		X

Dark-eyed Junco (*Junco hyemalis*)															X
Gray-headed Junco (*Junco caniceps*)	X	X	X	X		X	X	X	X	X	X	X	X	X	X
Chipping Sparrow (*Spizella passerina*)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
White-crowned Sparrow (*Zonotrichia leucophrys*)	X	X		X			X				X	X			X
Fox Sparrow (*Zonotrichia iliaca*)	X	X									X				X
Lincoln's Sparrow (*Zonotrichia lincolnii*)	X										X				X
Song Sparrow (*Zonotrichia melodia*)	X		X							X	X				X
Totals	61	52	44	50	25	29	42	19	34	46	64	42	41	49	80